

THE CARBONIFEROUS CORAL *PALAEACIS* IN IRELAND

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ABSTRACT. The tabulate coral *Palaeacis* Haime, 1857 is common in North America, but in Europe only two indigenous species occur, both in Ireland. *P. Smythi* Hudson, 1966 is distinguished from *P. axinoides* Smyth, 1929 by having only two corallites and a non-adherent corallum. *P. sp. nov.* has a conical corallum with a single corallite. These species have limited stratigraphical ranges in the Courceyan and basal Chadian stages and are useful zonal indices.

PALAEACIS, usually regarded as a tabulate coral, was founded posthumously by Haime in Milne-Edwards (1857, p. 9) for small wedge-shaped colonial corals from the Lower Carboniferous of North America. Many additional species have since been discovered in North America (see below), but only six species occur elsewhere; two of these are from Ireland.

North America

Haime's genus was based on a single species, *P. cuneiformis*, from the Lower Carboniferous of Indiana (see Milne-Edwards 1860, p. 171). Soon afterwards Meek and Worthen (1860) referred four similar corals also from the Lower Carboniferous of Indiana and Illinois to *Sphenopoterium*, but the identity of these (*S. cuneatum*, *S. enorme*, *S. obtusum*, and *S. compressum*, plus *S. enorme* var. *depressum* described in 1866) with *Palaeacis* (and indeed of *P. cuneiformis* with *S. cuneatum*) was proved by von Seebach (1866, p. 306), who himself described *P. cymba* (1866, p. 309) and *P. umbonata* (1866, p. 309) from the Lower Carboniferous of Iowa. (Kunth (1869, p. 188) later showed these to be synonyms of *S. obtusum*.)

Additional American species have been described from the Lower Carboniferous (Mississippian) by Miller (1892, p. 614) from Indiana (*P. cavernosa*), by Weller (1909, p. 277) from Missouri (*P. bifidus*), by Girty (1910, p. 190) from Arkansas (*P. carinata*), by Snider (1915, p. 70) from Oklahoma (*P. cuneata*), and by Easton (1944, p. 56) from Missouri (*P. conica*). Upper Carboniferous (Pennsylvanian) species have been described by Moore and Jeffords (1945, pp. 195–197) from Texas (*P. testata* and *P. walcotti*) and by Jeffords (1955, p. 11) from New Mexico (*P. kingi*).

Other North American records are summarized by Jeffords (1955, p. 9), who considered that *S. depressum* was synonymous with *S. enorme*, that *S. compressum* was synonymous with *S. obtusum*, and that *P. cuneata* was synonymous with *P. carinata*. Finally, Conkin, Bratcher and Conkin (1976, p. 4; 1978, p. 4) considered that *P. cavernosa* was synonymous with *S. obtusum*.

Europe

American species were discovered in Europe by Perceval (1876, p. 267), who recorded *P. cuneiformis* from the Lower Carboniferous of Bristol. The first European species referred to *Palaeacis* were Kunth's (1869, p. 185) record of *Ptychochartocyathus laxus* Ludwig (1866, pp. 189, 231) from the Lower Carboniferous of Hausdorf, Silesia, and de Koninck's (1872, p. 159) record of *Hydnopora cyclostoma* Phillips (1836, p. 202) from the Lower Carboniferous of Tournai, Belgium, and Northumberland. These species, now considered synonymous, were, however, rejected from *Palaeacis* by Hinde (1896, p. 446) and referred to *Microcyathus*.

Etheridge (1873, pp. 86, 97) described *P. compressa* var. *irregularis* from the Lower Carboniferous of Lanarkshire, but later (Etheridge and Nicholson 1878, p. 210) doubted its affinities.

Etheridge and Nicholson (1878, p. 224) described *P. cyclostoma koninckii* from the Lower Carboniferous of Tournai, Belgium, but this also now belongs to *Microcyathus*.

Hinde (1896, p. 440) described *P. humilis* from the Lower Carboniferous of Lancashire and Devon, which was also rejected from *Palaeacis* by Smyth (1929, p. 133) and placed in *Microcyathus* (see Jeffords 1955, p. 10).

The only indigenous European species of *Palaeacis* are therefore those from the Lower Carboniferous of County Wexford, Ireland, described by Smyth (1929, p. 126) as *P. axinoides* and by Hudson in Hudson, Clarke and Sevastopulo (1966, p. 257) as *P. axinoides smythi*.

Africa, Australasia, and Asia

The genus was recognized in Africa by Termier and Termier (1950, p. 81), who described *P. mauretanicus* from the Lower Carboniferous of Mauretania.

In Australasia Hill (1934, p. 100) discovered the American species, *P. cuneiformis*, from the Lower Carboniferous of Queensland, and Gerth (1921, pp. 120–122) described two indigenous species, *P. regularis* and *P. tubifer*, from the Permian of Timor Island.

Finally, Chudinova (1976, p. 33) recently discovered *Palaeacis* in Russia and described *P. formosa* from the Middle Carboniferous of the southern Verkhoyansk region, northern Siberia.

IRISH RECORDS OF *PALAEACIS*

The first records from Ireland were by de Koninck (1872, p. 158), Etheridge and Nicholson (1878, p. 221), Roemer (1883, p. 517), and Hinde (1896, p. 446), who all listed specimens from 'Hook Point' [= Hook Head], County Wexford, as *P. obtusa* (Meek and Worthen 1860). Smyth (1929, p. 126), after a detailed study of Hook Head material, however, referred the Irish specimens to a new species, *P. axinoides*, which has since been recorded from the Donegal Syncline by George and Oswald (1957, p. 172), and from a borehole at Ballyvergin, County Clare, by Hudson and Sevastopulo (1966, p. 296). I have traced only one of George and Oswald's specimens (HM C7739a, b), which is *Microcyathus cyclostoma* (Phillips).

Smyth (1929, p. 132) also described *Palaeacis* from two particular horizons at Hook Head which differed by possessing only two corallites. Hudson in Hudson, Clarke and Sevastopulo (1966, p. 257) found a similar two-corallite form at Feltrim Quarry, County Dublin, and referred these to a new subspecies, *P. axinoides smythi*. Hudson (1966, p. 256) also described a one-corallite specimen from Feltrim Quarry as *Palaeacis* sp. nov.

In addition to these published occurrences *P. axinoides* has recently been recorded from boreholes at Scagh (near Nenagh), County Tipperary (Irish Nat. Grid Ref. R830733) (I. D. Somerville, pers. comm. 1981). Knocktopher, County Kilkenny (Irish Nat. Grid Ref. S538376) (G. Ll. Jones, pers. comm. 1981), and Pallaskenry (near Askeaton), County Limerick (Irish Nat. Grid Ref. R415534) (G. Ll. Jones, pers. comm. 1981). *P. smythi* has recently been collected at Newtown Castle (near Callan), County Kilkenny (Irish Nat. Grid Ref. S464437) (G. Ll. Jones, pers. comm. 1981), Charlestown, County Kilkenny (Irish Nat. Grid Ref. S605177) (M. L. Keeley, pers. comm. 1979), and from a borehole at Moate, County Westmeath (Irish Nat. Grid Ref. N271490). Finally, *P. sp.* has been recorded from a number of boreholes near Silvermines, County Tipperary (Irish Nat. Grid Ref. R840712, R835712) (I. D. Somerville, pers. comm. 1981).

The Irish specimens mentioned herein are deposited in the Geological Museum of Trinity College, Dublin (TCD), the National Museum of Ireland, Dublin (NMI), the British Museum (Natural History), London (BM), and the Hunterian Museum, Glasgow (HM).

Stratigraphical occurrence

Because no formal chronostratigraphical division of the British and Irish Courceyan Stage has been agreed, the stratigraphical occurrence of *Palaeacis* in Ireland is reviewed using the informal chronostratigraphical subdivisions introduced by Sevastopulo (1979). 'Courceyan 1' is coextensive with the VI Miospore Subzone of Clayton *et al.* (1978); 'Courceyan 2' is defined by the base of the PC

Miospore Zone and has its upper limit at the extinction of siphonodellid conodonts; 'Courceyan 3' is equivalent to the *Polygnathus communis carina* Conodont Zone of Groessens (1977); 'Courceyan 4' is equivalent to the *Scaliognathus anchoralis* Conodont Zone and extends to the base of the Chadian.

P. axinoides. Smyth's (1929, 1930) records of *P. axinoides* from Hook Head span much of the marine succession which is entirely Courceyan in age. Text-fig. 1 shows Smyth's lithostratigraphical divisions, the revised nomenclature of Sleeman *et al.* (1974), and their relationship with the Courceyan subdivisions referred to above, based on palynological and conodont work at Hook Head by Higgs (1975), Clayton *et al.* (1977), and Johnston and Higgins (1981).

Smyth's lowermost record (as *Palaeacis* sp.), from the Grey Sandstone Group (1930, p. 539), corresponds to the upper part of the Houseland Sandstone Member of the Porter's Gate Formation (text-fig. 1*a, b*), and this horizon lies near the base of Courceyan 2 (text-fig. 1*c*). Smyth (1930, pp. 539, 540) also recorded the species from the succeeding Fish Shales and *Michelinia favosa* Beds, which are equivalent to Sleeman's (1974) Lyraun Cove Shale Member of the Porter's Gate Formation, and the lower part of the Hook Head Formation respectively (text-fig. 1*a, b*). The succeeding Bullockpark Bay Dolomite Member is devoid of fossils, but *P. axinoides* makes its last appearance at Hook Head (Smyth 1930, p. 541) 12 m below the top of the Supra Dolomite Beds (= upper part of the Hook Head Formation) (text-fig. 1*a, b*), which lies within Courceyan 3 (text-fig. 1*c*).

The borehole specimens are consistent with this range: that from Knocktopher occurs 1.7 m above the base of the Lyraun Cove Shale Member (text-fig. 1*b, c*) in Courceyan 2 (G. Ll. Jones, pers. comm. 1981); that from Pallaskenry occurs 12 m above the base of the Ringmoyle Shales, which are approximately equivalent to the Lyraun Cove Shales (G. Ll. Jones, pers. comm. 1981); those from Ballyvergin occur 4 m below and 12 m above the 'Ballyvergin Shale', which, according to conodont evidence of Clayton *et al.* (1980, pp. 85–89), would lie within Courceyan 2 and 3 respectively; finally, that from Scagh also occurs in Courceyan 2, 1 m below the 'Ballyvergin Shale' (I. D. Somerville, pers. comm. 1981).

P. smythi. Smyth's (1929, p. 132; 1930, p. 542) records of *P. axinoides* from the *Chonetes* Beds, at the top of the Hook Head Formation (text-fig. 1*a, b*), are shown herein to belong to *P. smythi*. This species therefore appears at Hook Head soon after the last appearance of *P. axinoides* in the upper part of Courceyan 3 (text-fig. 1*c*).

The specimen from Charlestown occurs in the Iverk Limestone Member, which is also Courceyan 3 (M. L. Keeley, pers. comm. 1979), that from Newtown Castle is from the Mallardstown Member, which is either Courceyan 3 or 4 (G. Ll. Jones, pers. comm. 1981), while that from the Moate borehole (depth 112 m) is certainly from Courceyan 4 (B. M. Thornbury, pers. comm. 1981).

The exact age of the specimens from Feltrim Quarry is difficult to ascertain; palynological samples from the Cover Shales, in which they occur, have been barren and conodont extractions have not been completely conclusive. The latter indicate either Courceyan 4 or early Chadian (Marchant 1978, p. 53), but on the basis of regional correlation they are more likely to be earliest Chadian (T. R. Marchant, pers. comm. 1979).

P. sp. nov. Conodonts from the Intra-Reef Shales of Feltrim Quarry, which have yielded the only known occurrence of this species, suggest that *P. sp. nov.* is of Courceyan 4 age (Marchant 1978, p. 53).

SYSTEMATIC PALAEONTOLOGY

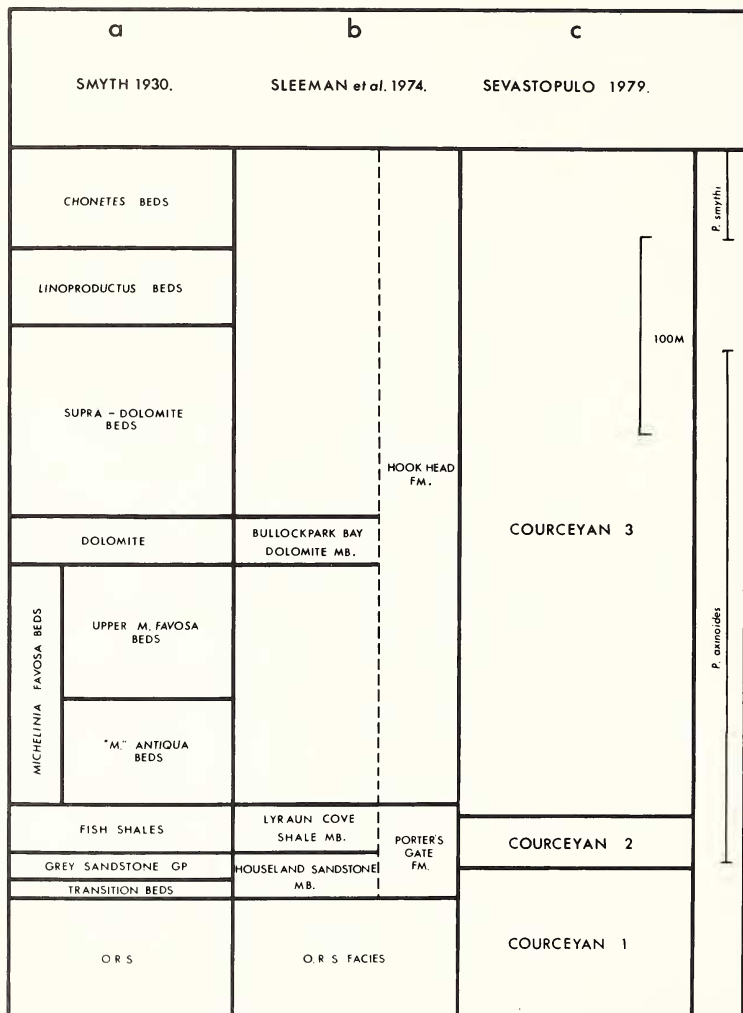
Class ANTHOZOA Ehrenberg, 1831

Order TABULATA Milne-Edwards and Haime, 1850

Family PALAEACIDAE Roemer, 1883

[*nom. correct.* Miller, 1889 ex Palaeaciden Roemer, 1883.]

Family name. Moore and Jeffords (1945, p. 195) proposed Palaeacidae, but it was already available. Hill and Stumm (1956, p. 466) credited it to Pošta (1902) and Jeffords (1955, p. 8) credited it to Miller (1892), but it was



TEXT-FIG. 1. Lithostratigraphical succession at Hook Head, County Wexford (columns *a*, *b*), with chronostratigraphical subdivisions (column *c*) and range of *Palaeacis axinoides* and *P. smythi*. GP = Group, MB = Member, FM = Formation.

first used in this form by Miller (1889, p. 153), and had already been used in the vernacular by Roemer (1883, p. 515). Under the present Rules of Nomenclature (Article 11(eii)) Roemer is credited with the authorship.

Subfamily PALAEACINAE Roemer, 1883
Genus PALAEACIS Haime in Milne-Edwards, 1857

[*nom. correct.* Milne-Edwards, 1860 *ex Palaeacis* Haime in Milne-Edwards, 1857.][= *Sphenopoterium* Meek and Worthen, 1860; *Palaecis* Snider, 1915 (*nom. null.*); *Palaecis* Smith, 1930 (*nom. null.*).]

Diagnosis. Colonies small and wedge-shaped or conical; often adherent in young stages, but later free; few rounded, atabulate corallites radiate from base of colony. Walls thick, in two layers; internal wall of fibrous calcite, external wall of small calcite plates, both permeated by canals opening as pores. External surface of ridged coenenchyme; reproduction by lateral increase.

Type species. *Palaecis cuneiformis* Haime in Milne-Edwards 1857, p. 9, pl. E1; fig. 2*a-d*; designated by monotypy; from Salem Limestone, Salem Formation, Meramecian (Middle Mississippian), Spergen Hill, Washington County, Indiana, North America.

Discussion. The genus, as diagnosed herein, excludes *Microcyathus* Hinde (1896), which differs by its perforate internal wall, but is very closely allied. The relationship between these genera needs closer attention. *Ptychochartocyathus* Ludwig (1866) has also been identified with *Palaecis*, but its type species, *P. latus*, almost certainly belongs to *Microcyathus*.

Nomenclature. There has been controversy over the authorship of *Palaecis*, many works attributing it to Milne-Edwards (e.g. Roemer 1883, p. 515; Gerth 1921, p. 120; Smyth 1929, p. 125), as its first mention was one year after Haime's death, in Milne-Edwards (1857). There was initially no indication that the name should not be attributed to Milne-Edwards, but later (1860) he revealed that Haime had described it before his death in a '*note inédite*'. According to the Rules of Nomenclature (Article 50) this is sufficient to credit the genus to Haime. There has also been disagreement over the spelling; the original citation in 1857 being '*Palaeacis*'. In 1860 this was altered, presumably by Milne-Edwards, to '*Palaecis*', which appears twice in the index, and so must be considered as an intentional emendation. Although there is no verifiable evidence that Haime's original spelling was in error, it is reasonable to suppose that he derived the name from the Greek *palaaios* (= ancient) and *akis* (= barbed). The corallum of Haime's type species, *P. cuneiformis*, is barbed when viewed in profile. If, therefore, one regards Haime's spelling as an inadvertent error, Milne-Edwards's emendation becomes justified, and the usual spelling of *Palaecis* can be retained.

Palaecis axinoides Smyth, 1929

Plate 29, figs. 1–12, text-figs. 4*a, b, 5*

1929 *Palaecis axinoides*, sp. nov.; Smyth (*pars*), p. 126, pl. 6, figs. 1–9; pl. 7, figs. 1–9; pl. 8, figs. 1–8; *non* pl. 6, figs. 10–12 [which are *P. smythi* Hudson].

Diagnosis. Wedge-shaped *Palaecis* with up to twenty-four corallites. Normally adherent in young stages, with supporting bodies included in colony base.

Type specimens. Holotype, TCD T159, Pl. 29, figs. 1, 2; from Hook Head Formation, Courceyan Stage, Lower Carboniferous, 730 m ENE of lighthouse, Hook Head, County Wexford (Irish Nat. Grid Ref. X734973); original designation Smyth 1929, p. 126, pl. 6, fig. 1*a-c*.

Paratypes, BM R26151, BM R26152, NMI 98-1928; locality and horizon as for holotype; original designation Smyth 1929, p. 126.

Material. Over 400 specimens (TCD T159, F160–F167, F179–F190, 4648–4651, 4655–4658, 4660–4682, 4687–4696, 4702–4836, 4838–4841, 4843–4863, 4870–4922) from Hook Head, County Wexford. One specimen (TCD 19977) from Ballyvergin borehole, County Clare. [Hudson and Sevastopulo (1966, p. 296) listed two specimens from Ballyvergin, but the younger specimen is now missing from the collection.] One specimen from Scagh borehole, County Tipperary. One specimen (TCD 19981) from Knocktopher borehole, County Kilkenny. One specimen (TCD 19982) from Pallaskenry borehole, County Limerick.

Description. Corallum small and wedge-shaped with calices at the thicker end of the wedge. The lower peripheral margins are devoid of calices and diverge from the colony base at approximately 130°.

Number of corallites usually between two and fourteen, but as many as twenty-four have been observed; text-fig. 2 illustrates the frequency of specimens at each corallite stage. The two-corallite stage corallum attains a mean height of 6.8 mm, a mean width of 7.7 mm, and a mean thickness of 3.8 mm. These parameters increase in parallel during astogeny (text-fig. 3) and the largest colony recorded (23-corallite stage) had a height of 30.5 mm, a width of 33.7 mm, and a thickness of 16.2 mm.

External surface of the corallum has a characteristic ornament (Pl. 29, fig. 3) of irregular, sub-parallel, close-set ridges and grooves which run discontinuously down the sides of the corallum. They may be straight or sinuous and often bifurcate distally.

Corallites generally sub-circular, but may be polygonal, and reach a maximum diameter of 5–7 mm. Calices deep (up to 5 mm) with almost vertical inner walls marked by forty to fifty longitudinal septal ridges (Pl. 29, fig. 3). Concentric growth lines, normal to the septal ridges, may also occur (Pl. 29, fig. 3) so that the overall appearance is granular. The calice floor is flat, unornate, and tabulae do not occur.

Corallite wall usually 1–2 mm thick and consists of two layers (Pl. 29, figs. 6, 7). An internal layer forms the corallites' floors and walls (Pl. 29, fig. 6) and is composed of fibrous calcite. It is thick on the floors, but thins distally and in transverse section the septal ridges can be seen on its inner surface (Pl. 29, fig. 7). The external tissue forms an outer coating over the whole colony (Pl. 29, figs. 6, 7) and consequently corallite walls on the edge of the colony consist of two layers while those between corallites are composed only of internal tissue.

The external tissue is not fibrous, but is composed of successive calcite plates (200 μ m wide) (text-fig. 4a) normal to the colony surface. The surface expression of each plate is a ridge, and of each plate boundary is a groove, forming the characteristic surface ornament. Their microstructure was described in detail by Smyth (1929, pp. 128, 129).

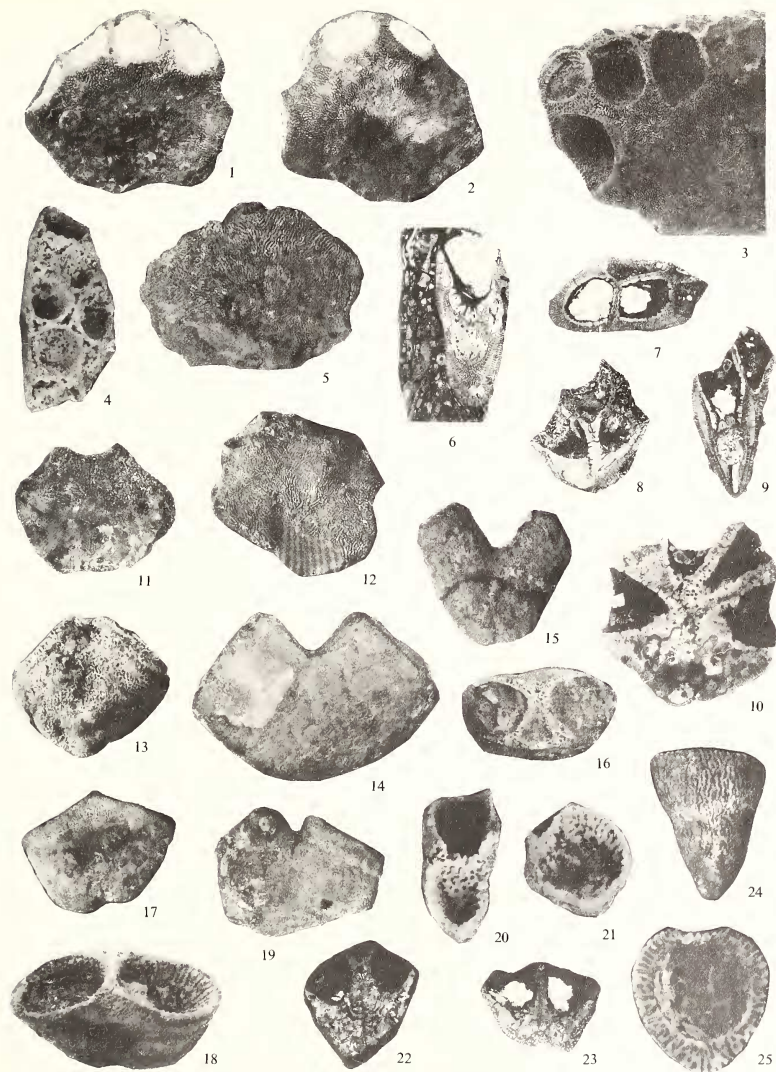
Corallite walls are penetrated by canals normal to the wall surface which pass through both layers of tissue (text-fig. 4a). In the external tissue they excavate the boundaries between adjacent plates and are 80–120 μ m wide. They join with canals in the internal tissue which are wider (up to 200 μ m) and often forked (Pl. 29, fig. 6). Canals also occur in the internal tissue between two corallites, and in the internal tissue of the corallite floor when they radiate downwards and outwards (Pl. 29, fig. 6).

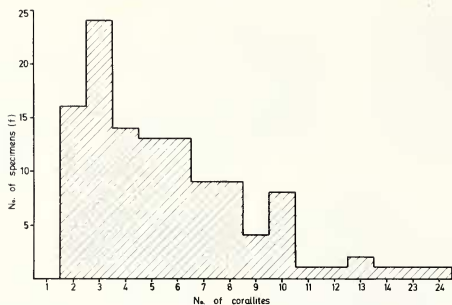
EXPLANATION OF PLATE 29

Figs. 1–12. *Palaeacis axinoides* Smyth, 1929. 1, 2, TCD T159 (holotype), lateral views with undistorted base in mature corallum, $\times 2$. 3, TCD F186, lateral view with external surface ornament of ridges and grooves and longitudinal septal ridges, concentric growth lines and pores in the calices, $\times 2$. 4, TCD 4884, apical view with pores on floor and walls of calice, $\times 2$. 5, TCD 4738a, lateral view with canals opening on to external surface as pores, $\times 2$. 6, TCD F181d, longitudinal thin section with two-layered corallite wall showing forked canals in internal tissue and calcite plates in external tissue, $\times 2$. 7, TCD F187b, transverse thin section with two-layered corallite wall and septal ridges on the internal layer, $\times 2$. 8, TCD F180, longitudinal thin section showing absence of foreign inclusion in base of corallum, $\times 2$. 9, 10, TCD F187d, TCD F179b, longitudinal thin sections with foreign inclusions in base of corallum, $\times 2$. 11, 12, TCD F165, TCD F182, lateral views with brachiopod shell fragments protruding from colony base, $\times 3$, $\times 2$. All specimens from Hook Head Formation, Courcean Stage, Lower Carboniferous, Hook Head, County Wexford.

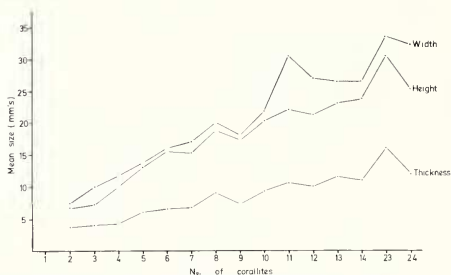
Figs. 13–23. *Palaeacis smythi* Hudson, 1966. 13, TCD F177 (holotype), lateral view with undistorted base to corallum and slight notch between distal portions of corallites, $\times 4$. 14, 15, TCD 19955, TCD F172, lateral views with corallites developed as well-separated branches, $\times 3$, $\times 2$. 16, TCD 4869, apical view with incipient third corallite, $\times 3$. 17, 18, TCD F169, lateral and oblique apical views showing growth lines on external surface, regular base to corallum, and septal ridges in calice, $\times 3$, $\times 4$. 19, TCD F171, lateral view with growth lines on external surface, $\times 3$. 20, TCD 4866j, apical view with pores on floor and walls of calice, $\times 4$. 21, TCD 4698, apical view of ? single corallite stage, $\times 5$. 22, 23, TCD 19979, TCD 19980, longitudinal thin sections with two-layered corallite wall and canals in both layers, $\times 2$. 13, 15–23 from Hook Head Formation, Courcean Stage, Lower Carboniferous, Hook Head, County Wexford; 14 from Cover Shales, ? Chadian Stage, Lower Carboniferous, Feltrim Quarry, County Dublin.

Figs. 24, 25. *Palaeacis* sp. nov. TCD 19511, lateral and apical views, $\times 4$, $\times 5$. From Intra-Reef Shales, Courcean Stage, Lower Carboniferous, Feltrim Quarry, County Dublin.





TEXT-FIG. 2. Frequency of specimens at each stage of corallite development in *Palaecis axinoides*.



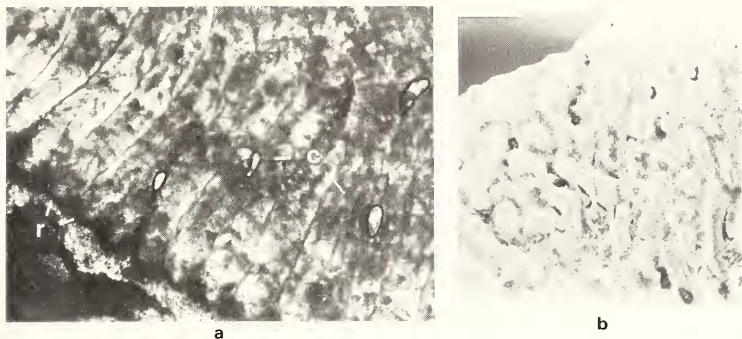
TEXT-FIG. 3. Growth of *Palaecis axinoides* related to each stage of corallite development.

All canals eventually open on to the external surface (Pl. 29, fig. 5) or into the calices as pores (Pl. 29, fig. 4). Externally they occur in the grooves of external tissue (text-fig. 4b), on the calice walls they occur between the septal ridges (Pl. 29, fig. 3), and on the calice floors they are disposed in a radial pattern (Pl. 29, fig. 4).

In longitudinal section a foreign inclusion is nearly always revealed proximally (Pl. 29, figs. 9, 10) and in immature examples it may protrude from the colony base. Brachiopod, bivalve, crinoid, and gastropod fragments have all been observed (Pl. 29, figs. 11, 12). In other immature coralla the inclusion is completely concealed, but is still discernible owing to its awkward shape distorting the colony base. Many coralla in the two, three, and four corallite stages have an irregular base, but in most mature specimens the inclusion is invisible externally and the colony base is regular (Pl. 29, fig. 1). Any irregularities due to its presence have become gradually masked by progressive thickening of the surrounding external tissue.

Longitudinal sectioning has, however, occasionally revealed an absence of any inclusion in both immature and mature examples (Pl. 29, fig. 8). In such two-, three-, and four-corallite coralla the colony base is perfectly regular.

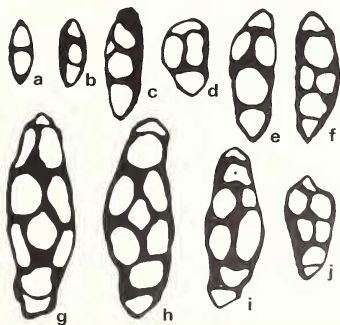
Astogeny. Development of the protocorallite. The foreign inclusion usually embedded in the colony base clearly formed a support during initial colony development. Settling planulae preferred the hard base that a shell fragment offered on which to commence protocorallite skeleton secretion. Growth lines in the external tissue parallel to the surface of the corallum suggest the tissue accreted by addition of layers to the external surface and,



TEXT-FIG. 4. *Palaeaxis axinoides* Smyth, 1929. *a*, TCD F181d, photomicrograph showing external layer of corallite wall consisting of successive calcite plates, each of which has a surface expression as a ridge (*r*), and canals excavating the boundaries between plates (*c*), $\times 36$; *b*, TCD 4660, SEM photograph showing pores on external surface (i.e. canal openings) occurring between the ridges of external tissue, $\times 20$.

therefore, that the surface was enveloped in coenosarc. The coenosarc gradually extended over the supporting shell fragment (Pl. 29, fig. 12), eventually spread under its lower surface, and finally fused, trapping the supporting body inside the colony. At this moment the colony ceased its adherent mode of life and became free. Envelopment of the supporting body was usually complete by the two-corallite stage, but up to fourteen corallites may have formed before this occurred. Some colonies detached themselves from the support before enveloping it, leaving a scar on the external surface which reflects the shape of the shell fragment.

Corallite addition. No specimens of a one-corallite stage of *P. axinoides* have been found (see *Remarks* on *P. sp. nov.*), probably because the first bud appeared after such a short period of protocorallite growth. (The smallest well-developed two-corallite stage recorded is only 2.5 mm in height.) Further increase of corallites is illustrated in text-fig. 5; the first three corallites form in a single row (as in type species, *P. cuneiformis* (see Conkin, Bratcher and Conkin 1976)), from the four- to eight-corallite stage new buds were added in two rows, and from the ninth corallite onwards a third row was initiated. Symmetry was maintained in the colony by the positioning of each



TEXT-FIG. 5. Camera-lucida drawing showing astogeny of *Palaeaxis axinoides* from the two-corallite stage to the ten-corallite stage, $\times 3.5$. *a*, TCD 4796, *b*, TCD 4902c, *c*, TCD 4902a, *d*, TCD 4702, *e*, TCD 4836, *f*, TCD 4838, *g*, TCD F163, *h*, TCD F161, *i*, TCD T159, *j*, TCD 4887.

new bud. This pattern (text-fig. 6) occurs consistently up to the seven-corallite stage. In the eight- to ten-corallite stages approximately half the observed specimens conform, but above this number no pattern was discernible, owing to an insufficiency of samples.



TEXT-FIG. 6. Frequency of specimens conforming to normal pattern of corallite development in *Palaeacis axinoides*.

Palaeacis smythi Hudson in Hudson, Clarke and Sevastopulo, 1966

Plate 29, figs. 13–23

- 1929 *Palaeacis axinoides*, sp. nov.; Smyth (*pars*), p. 126, pl. 6, figs. 10–12; *non* pl. 6, figs. 1–9; pl. 7, figs. 1–9; pl. 8, figs. 1–8 [which are *P. axinoides* Smyth].
 1966 *Palaeacis axinoides smythi* subsp. nov.; Hudson in Hudson, Clarke and Sevastopulo, p. 257.

Diagnosis. Wedge-shaped *Palaeacis* with only two corallites (rarely three) forming well-separated branches. Never adherent in young stages, no supporting bodies included in colony base.

Holotype. TCD F177, Pl. 29, fig. 13; from Hook Head Formation, Courceyan Stage, Lower Carboniferous, 230 m south-east of Slade Castle, Hook Head, County Wexford (Irish Nat. Grid Ref. X747985); original designation Hudson in Hudson, Clarke and Sevastopulo 1966, p. 257; figured Smyth 1929, pl. 6, fig. 11.

Material. Fifty-eight specimens (TCD F168–F178, 4683–4686, 4697–4701, 4864–4869, 19979, 19980) from Hook Head, County Wexford. Twenty-one specimens (TCD 19955–19975) from Feltrim Quarry, County Dublin. One specimen (TCD 19983) from Newtown Castle, County Kilkenny. One specimen (TCD 19976) from Charlestown, County Kilkenny. One specimen (TCD 19978) from Moate borehole, County Westmeath.

Description. Similar in most features (surface ornament, wall structure, and canal system) to *P. axinoides*, but number of corallites restricted to two almost without exception. These diverge from the colony base at a mean angle of 120° in the Feltrim sample, and at 65° in the Hook Head sample.

From Hook Head (see Smyth 1929, p. 132) thirty-seven out of forty specimens possess two corallites and at Feltrim seventeen out of twenty-one are likewise. In the three exceptions from Hook Head one has a well-developed third corallite (figured Smyth 1929, pl. 6, fig. 12), one has an incipient bud between the first two corallites (Pl. 29, fig. 16), and the other is apparently a single corallite (Pl. 29, fig. 21). In the four exceptions from Feltrim one has a well-developed third corallite between the first two corallites, while in the others the third 'corallites' are small, secondary apertures opening on the sides of the two main branches.

The absence of a third corallite between the first two, coupled with their continued divergence, resulted in the eventual separation of the first two corallites and the development of two elongated branches, the margins of which are free. This feature is common in Feltrim specimens (Pl. 29, fig. 14), but rare at Hook Head (Pl. 29, fig. 15), where often only a slight notch developed (Pl. 29, fig. 13).

The corallum has a mean height of 8.0 mm at Hook Head and 9.0 mm at Feltrim, a mean width of 9.9 mm at Hook Head and 12.3 mm at Feltrim, and a mean thickness of 4.2 mm at Hook Head and 5.3 mm at Feltrim.

Corallites oval when in contact at the colony base, but after separation become circular and reach a mean diameter of 5.8 mm. Calices deep (up to 4 mm), the steep inner walls marked with concentric growth lines and about fifty longitudinal septal ridges (Pl. 29, fig. 18).

Unfortunately, the specimens from Hook Head and Feltrim have been silicified and their microstructure destroyed. However, the least altered coralla (Pl. 29, fig. 23) suggest an external tissue composed of calcite plates as in *P. axinoides* and a thick internal tissue (Pl. 29, figs. 22, 23). Canals in both layers of tissue more numerous than in *P. axinoides*. Almost every boundary between the plates of external tissue is excavated by a canal (80–120 μ m wide) which passes into a wider canal (200 μ m wide) in the internal tissue (Pl. 29, fig. 23).

Longitudinal sectioning of numerous coralla has revealed an absence of included supporting bodies. Consequently, the colony base is not distorted by accommodating awkward-shaped objects, and instead is perfectly regular. The contours of the protocorallite and its offset are clearly visible (Pl. 29, fig. 17), the latter disposed slightly above the former, and separated from it by a slight notch.

Asotogeny. Records of a one-corallite stage in *Palaeacis* are rare (see *Remarks* on *P. sp. nov.*), but one specimen from Hook Head, a shallow cup 2.5 mm high and 3.5 mm in diameter, appears to consist of a single corallite (Pl. 29, fig. 21). The second corallite usually appears much sooner, sometimes when the protocorallite is only 0.5 mm high, and the early two-corallite stage is similar to that of *P. axinoides* except for its regular base (Pl. 29, fig. 13). The late two-corallite stage, with its corallites as separate branches (Pl. 29, fig. 14), is usually the most advanced astogenetic stage reached. Rarely a third corallite develops in the space created by the divergence of the first two (Pl. 29, fig. 16).

Discussion. Specimens of this species were described by Smyth (1929, p. 132) from two horizons in the *Chonetes* Beds at the top of the Hook Head succession in County Wexford (text-fig. 1a), differing from typical *P. axinoides* in several respects:

1. Most possess only two corallites and none possesses more than three.
2. Corallites grow as separate independent branches.
3. Most are larger than typical two-corallite specimens of *P. axinoides* (height, width, thickness).
4. No evidence that they were adherent in young stages; supporting bodies are not found at the colony base, which is regular and undistorted.

Smyth (1929) doubted that they belonged to a separate species and argued that they were stunted forms of *P. axinoides* responding to an unfavourable environment; other species in these beds (e.g. *Vaughania vetus* Smyth, 1927) were also dwarfed. Either genetic control or phenotypic variation could explain the differences listed above. If a colony is restricted to two corallites (either genetically or ecologically), and if those corallites continue to grow, they will also continue to diverge and will eventually separate as independent branches. They will also be larger (height, width, and thickness) than typical two-corallite members of *P. axinoides*.

Phenotypic variation cannot explain the absence of an included supporting body. Suitable supports were certainly available, as *V. vetus* is found in the same beds attached to brachiopod and bivalve shells. Smyth considered that the support had been obscured by silification, but in these beds it is not intense and in any case the regular colony base provides external evidence of its absence. *P. axinoides* does sometimes lack such a support, but there seems no reason why stunting should only affect the few non-adherent colonies. One might also expect an ecological stunting to have more effect on corallite size than on colony size (i.e. one would not expect the almost total restriction to two corallites). It seems more likely that these two-corallite forms are a distinct species, genetically restricted to two corallites by a mutation which affected a sample of non-adherent *P. axinoides*. Their distinct stratigraphical occurrence supports this theory. Hudson in Hudson, Clarke and Sevastopulo (1966, p. 257) found a similar two-corallite fauna at Feltrim Quarry, County Dublin, likened them to those from Hook Head, and, believing corallite number to be worthy at least of sub-specific separation, described them as *P. axinoides smythi*, which is here elevated to specific level.

P. smythi is similar to the American *P. bifidus* from the Lower Carboniferous of Missouri (Weller 1909, p. 277), which is also restricted to two corallites and has a comparable morphology. It is slightly larger in size, but specimens figured by Weller (1909, pl. 10, figs. 8–11) are very close to some from

Feltrim Quarry. *P. conica* (Easton 1944, p. 56), from the Lower Carboniferous of Missouri, also has two corallites, but the corallum is conical and not wedge-shaped (see *P. sp. nov.*).

In Ireland this species is most similar to *P. axinoides*. Mature examples are easily distinguishable as *P. axinoides* has more than two corallites. Immature specimens of *P. smythi*, before corallite separation, are, however, very similar to immature two-corallite *P. axinoides*. Distinction is still usually possible as *P. axinoides* normally has an included supporting body and consequently an irregular base; *P. smythi* has no such inclusion and a regular base. Occasionally *P. axinoides* does not possess a supporting body, in which case the two-corallite stage is indistinguishable from immature *P. smythi*. Separation is then only possible by examination of a population; *P. smythi* is characterized by an almost total domination of two-corallite stages, whereas *P. axinoides* exhibits a frequency distribution of corallite stages as shown in text-fig. 2.

Palaeacis sp. nov.

Plate 29, figs. 24, 25; text-fig. 7

1966 *Palaeacis* sp. nov.; Hudson in Hudson, Clarke and Sevastopulo, p. 256.

Diagnosis. Conical *Palaeacis* with a single corallite. ?Not adherent in young stages, no supporting bodies included in colony base.

Material. One specimen (TCD 19511) from Feltrim Quarry, County Dublin.

Description. Corallum consists of a single conical corallite, 6.8 mm high, the sides diverging from the apex at about 40° (Pl. 29, fig. 24). Two transverse constrictions on the outer surface, approximately 2 mm and 4 mm from the base, may represent external growth lines. The base tapers to a fine point, which is broken in the only available specimen, but the corallum is almost complete and there is no evidence of any scar of attachment to a supporting body.

The external surface ornament of ridges and grooves is identical to other species of *Palaeacis*, but the single specimen has been polished distally, so details of the calice are not known. In transverse section, however, the corallite is sub-circular with a maximum diameter of 5.9 mm (Pl. 29, fig. 25). There is no axial structure, but projecting into the calice from the wall are a number of random extensions (right-hand side of text-fig. 7) comparable to the septal ridges of *P. axinoides* and *P. smythi*.

The wall is up to 1.2 mm thick, and is regularly traversed by numerous canals (120 µm wide) normal to the wall surface (text-fig. 7), which open interiorly and exteriorly as pores. Externally they always occur in the grooves of external tissue (text-fig. 7).

The preservation is such that it is impossible to elucidate wall microstructure, but septal ridges in the calices suggest a similarity with the internal tissue of *P. axinoides* and *P. smythi*, while the regular canals, their magnitude and consistent position opposite external grooves, recall the external tissue of these species. In this specimen the canal walls would correspond to the plates of external tissue described on p. 216 and would be of the order of 200 µm in width, comparable to those in *P. axinoides*. In other words, the corallite wall in *P. sp. nov.* is probably double-layered as in other species of *Palaeacis*.



TEXT-FIG. 7. Camera-lucida drawing of transverse section of *Palaeacis* sp. nov. showing numerous canals in corallite wall and ? septal ridges extending into calice (right side), $\times 8$.

Discussion. There is too little material for adequate sectioning, and there is accordingly no direct evidence of tabulae and supporting bodies, or the wall structure. It is safe to assume that tabulae do not exist; there is no trace of them in the one transverse section and they are unknown in *Palaeacis*. It is also unlikely that a supporting body is included in the colony base; this tapers to a fine point while a supporting body would distort it as in *P. axinoides*.

Specimens of *Palaeacis* with one corallite are rare: Conkin, Bratcher and Conkin (1976, p. 13) alleged that Smyth (1929, p. 130) recorded a one-corallite stage of *P. axinoides*, but he was actually describing a postulated astogeny deduced from growth lines on mature specimens. Etheridge and Nicholson (1878, p. 222) mentioned a one-corallite stage of '*P.*' *cyclostoma*, and Hinde (1896, p. 441, pl. 23, fig. 7) figured a one-corallite stage of '*P.*' *humilis*, but these are both now placed in *Microcyathus*. The only unquestionable records are those of Williams (1943, p. 59) and Conkin, Bratcher and Conkin (1976, p. 13), who reported one-corallite stages in *P. enormis* and *P. cuneiformis* respectively, and the description in this paper of a one-corallite stage of *P. smythi*. In all three cases the specimens were interpreted as the first astogenetic stage of a colonial species, but with *P. sp. nov.* there are three possible explanations: (1) It could be a one-corallite stage of the colonial *P. smythi*, the only other species present at Feltrim. This is untenable because the one-corallite stage of *P. smythi* is a shallow, rounded cup (Pl. 29, fig. 21), not a slender, pointed cone, and never attains a height of 6 mm before budding. (2) It could be the one-corallite astogenetic stage of another colonial species yet unrecorded from Feltrim. *P. conica* (Easton 1944, p. 56), from the Kinderhookian of the Mississippi Valley, has a comparable conical corallum and only differs from the Feltrim specimen in possessing a small secondary corallite at the distal end of the cone. It is possible that the Feltrim specimen is an example of *P. conica* that has not yet budded. *P. conica*, known from only two specimens, is 12 mm in height. The fact that no other American species are known from Ireland, and vice versa, suggests, however, that the two are unlikely to be conspecific and *P. sp. nov.* is more probably a separate species which has evolved a conical colony by homeomorphy. (3) The final explanation is that this is a solitary species of *Palaeacis*. As such it would be unique amongst the tabulate corals, which are generally considered an exclusively colonial group. Conversely, the existence of solitary *Palaeacis* might suggest that the genus is not a tabulate coral.

Whether it is solitary, or whether it is a colonial species awaiting its first bud, is impossible to determine until more material is available. However, its gross morphology is so unlike any astogenetic stage of either *P. axinoides* or *P. smythi* that it is here considered a distinct species.

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